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Flavor Perception and Preference Development in Human Infants

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FOCUS

Responses to basic tastes are remarkably similar across cultures and species, which suggests these responses are a product of children's basic biology

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Flavor Perception and Preference Development in Human Infants

by Catherine A. Forestell

Key insights

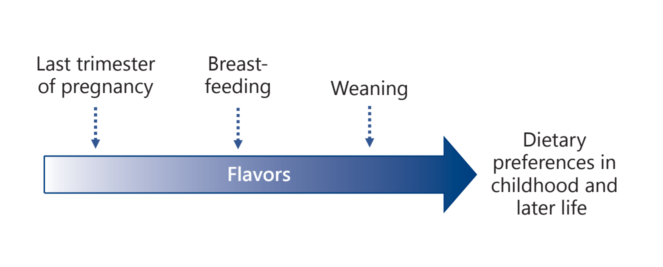
Children's innate dietary preferences are a reflection of our basic biology, which drives the inclination towards sweet items and the avoidance of bitter-tasting items such as green leafy vegetables. Once essential for our survival, this adaptive mechanism is now at odds with an environment overloaded with unhealthy foods. Nevertheless, this biological predisposition can be overcome by modulating early flavor experiences during gestation, breastfeeding, and weaning.

Current knowledge

In comparison to other senses such as sight and sound, the sense of taste begins to emerge early. During the last trimester of prenatal development, taste buds are already capable of detecting and transmitting information to the central nervous system. The intrauterine environment is rich in flavors that change according to the mother's diet. The fetus actively swallows between 500 and 1,000 mL of amniotic fluid per day during the last trimester. After birth, the flavors from the maternal diet continue to be transmitted to the infant via breast milk. This ongoing exposure to flavors guides the infant's taste preferences and sets the foundation for dietary choices made in later childhood.

Practical implications

Pregnant and nursing women should be encouraged to consume a healthy diet that includes a variety of flavors. Early exposure of the developing fetus or young infant to flavors associated with fruits and vegetables can shape food and flavour preferences, thereby increasing the infant's acceptance of healthy foods in the environment. Repeated exposure to healthy foods at weaning will reinforce and expand these preferences.



Flavor experiences begin during prenatal development and form a continuum that lasts into later childhood. This shapes an individual's dietary preferences in later life.

Recommended reading

Siega-Riz AM, Deming DM, Reidy KC, Fox MK, Condon E, Briefel RR: Food consumption patterns of infants and toddlers: where are we now? J Am Diet Assoc 2010;110:S38–S51.

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Flavor Perception and Preference Development in Human Infants

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Key Messages

- Children's dietary habits reflect their basic biology, which predisposes them to prefer sweet tastes and to avoid bitter-tasting foods such as green leafy vegetables. Although once adaptive, in modern food environments children's proclivity for unhealthful foods can place them at risk for obesity and a number of diseases.
- Flavors from the mother's diet are transmitted to amniotic fluid and breast milk, and children have repeated and varied opportunities to learn to like the flavors of healthful foods they will likely encounter during weaning.
- At weaning, 8–10 exposures to a food will increase intake even if the food is initially rejected; further exposures may be required to increase liking. Exposing infants to a variety of flavors promotes infants' willingness to consume novel foods.

Keywords
Bitter · Sweet · Taste · Flavor · Sensory learning · Breastfeeding · Formula feeding · Fruit · Vegetables

Abstract
As most parents and caregivers are aware, feeding children a nutritionally balanced diet can be challenging. Children are born with a biological predisposition to prefer sweet and to avoid bitter foods such as green leafy vegetables. It has been hypothesized that this predisposition evolved to attract children to energy-dense foods while discouraging the consumption of toxins. Although this may have enhanced survival in environments historically characterized by food scarcity, it is clearly maladaptive in many of today's food environments where children are surrounded by an abundance of sweet-tasting, unhealthful foods and beverages that place them at risk for excessive weight gain. Because overweight or obese children tend to become overweight or obese adults who are at risk for a range of cardiovascular diseases, it is of primary importance to develop effective evidence-based strategies to promote the development of healthy eating styles. Fortunately, accumulating evidence

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suggests that, starting before birth and continuing throughout development, there are repeated and varied opportunities for children to learn to enjoy the flavors of healthful foods. Because flavors are transmitted from the maternal diet to amniotic fluid and breast milk, mothers who consume a variety of healthful foods throughout pregnancy and lactation provide their infants with an opportunity to learn to like these flavors. This in turn eases the transition to healthful foods at weaning. In contrast, infants fed formula learn to prefer its invariant flavor profile, which differs from breast milk, and may initially be less accepting of flavors not found in formula. This process can continue throughout weaning and into childhood if infants are repeatedly exposed to a variety of healthful foods, even if they initially dislike them. These early-life sensory experiences establish food preferences and dietary patterns that set the stage for lifelong dietary habits.

Introduction

Parents and caregivers face the ubiquitous challenge of providing their children with a balanced diet that promotes healthy growth and development. The USDA [1] recommends that families meet this challenge by feeding children a diverse, nutrient-dense diet that contains vegetables, fruits, whole grains, low-fat dairy products, and quality protein sources. As many parents lament, meeting these dietary recommendations is difficult for a number of reasons – not the least of which is that children tend to dislike vegetables and prefer sugar-sweetened foods and beverages. As a result, children generally avoid eating most vegetables and forgo consumption of natural sources of sugars such as fruit in favor of foods and beverages that are high in added sugars [2, 3]. This preference for simple sugars and energy-dense foods over nutrient-rich alternatives has dire health consequences. Children's poor dietary habits are a risk factor for several diseases, including pediatric obesity, type 2 diabetes, and hypertension, which have traditionally afflicted older adults [4, 5].

Children's poor dietary habits are a risk factor for several diseases, including pediatric obesity, type 2 diabetes, and hypertension

This article provides an understanding of why children prefer or dislike certain foods and how we can shift their inborn preferences through early sensory experience. It begins with a brief overview of the ontogeny of sweet and bitter taste perception, both of which have important functional significance in children's consumption of healthful, bitter-tasting vegetables and unhealthful, sweet-tasting desserts and beverages. It then reviews how early flavor experiences interact with the plasticity of the chemosensory system to shift children's preferences and acceptance of fruit and vegetables. In sum, this research shows that, although children are born with biological predispositions to prefer highly sweet-tasting foods and beverages over healthful, less sweet alternatives, their preferences can be altered by early experiences from gestation through weaning and do not necessarily determine lifelong dietary habits.

Taste and Flavor Perception

Flavor is a powerful determinant of human consummatory behavior. Although in everyday language the terms *flavor* and *taste* are often used interchangeably, flavor refers to the integrated sensation that arises from the combined input of taste, chemosensation, and olfaction [6]. For example, when we consume an orange soda, sugars and citric acid come into contact with taste receptors throughout the oral cavity and the gut, which send messages to the brain that allow us to perceive the sweet and sour taste of this beverage. We also experience the bite of carbon dioxide, which activates trigeminal nerve fibers that innervate the nasal and oral cavity, triggering chemosensation. In addition, the citrus odor travels retronasally along the back of the nasopharynx toward the roof of the nasal cavity, reaching olfactory receptors located in the epithelium of the nasal cavity. Unlike the limited number of primary tastes, which consist of sweet, sour, bitter, savory, and salty, there are thousands of distinctive odors with separable sensations that allow us to experience a rich array of flavors.

Relative to other sensory capacities such as vision and audition, the sense of taste begins to emerge relatively early. Behavioral studies using a variety of techniques suggest that by the last trimester of prenatal development taste buds are capable of detecting and communicating information to central nervous system structures responsible for organizing and controlling affective behaviors (for a more extensive review see [7]). Similarly, the olfactory bulb and receptor cells are functional by the last trimester. Given the extensive prenatal development of the chemosensory system, it is not surprising that the newborn is sensitive and responsive to odor, taste, and flavor stimuli at birth.

Fig. 1. Newborn's orofacial responses to the sweet taste of 0.73 M sucrose (left) and the bitter taste of 0.003 M quinine (right) presented approximately 2 h after birth, before the first postnatal feed. Using a syringe, 0.2 mL of each taste solution at room temperature was presented to the central portion of the dorsal surface of the infant's tongue. Reprinted with permission from [15].

Age-Related Changes in Response to Sweet and Bitter Taste

Accumulating research suggests that preferences for basic tastes are a major determinant of children's food choices and acceptance patterns [8–11]. Over the past few decades, our understanding of children's perception and preference for basic tastes has grown substantially (for a review see [7]). We now know that children live in their own sensory world, with their sensitivities and preferences for tastes changing throughout childhood. Responses to basic tastes are remarkably similar across cultures and species, which suggests these responses are a product of children's basic biology.

Sweet Taste

In nature, most sugars (e.g., fructose, maltose, and sucrose) have a small molecular weight and are found primarily in plants. These sugars provide sources of glucose, a key source of energy. For infants, the sweet sugar lactose found in breast milk can also be metabolized to provide glucose energy. Indirect evidence from early studies of fetuses [12], together with findings from studies of premature infants, suggests that detection of sweet taste stimuli is possible during late gestation [13]. This early experience may prepare newborns to detect and accept the basic taste of sweet found in breast milk, which contributes to their survival.

Palatable tastes, such as sucrose, are thought to induce sensory pleasure, which elicits appetitive reactions. As shown in Figure 1, tasting 0.73 M sucrose elicits facial relaxation, sucking movements, and sometimes smiling in newborns, as first described by Steiner [14] and later by Rosenstein and Oster [15]. Consistent with this, research has repeatedly demonstrated that infants preferentially consume sweet-tasting solutions relative to water and can differentiate varying degrees of sweetness (0.05–0.30 M) and different kinds of sugars; sucrose, fructose, glucose, and lactose [16]. These findings converge with physiological findings; for example, administration of drops of aqueous sucrose (0.73 M) to the tongues of newborn infants produced greater relative left-side activation in both frontal and parietal regions of the brain, which is considered to be a reliable indicator of positive emotion [17].

Compared to adults, who on average prefer 0.44 M sucrose, 5- to 10-year-old children have a much sweeter tooth, preferring 0.54 M sucrose [18], almost double the concentration of most soft drinks [19]. The higher preference for sucrose observed throughout childhood may be related to rapid physical growth during this time [20]. This hypothesis is supported by evidence that adolescents with higher sweet preferences also have higher levels of a biomarker for bone growth than do those with lower sweet preferences [21]. Because this biomarker increases during growth spurts, age-related declines in preference for sweet taste may correspond with cessation of physical growth [22, 23].

Bitter Taste

In contrast to sweet taste, bitter taste appears to be disliked by infants at birth; as shown in Figure 1, they gape

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when a bitter quinine solution (0.003 M) or urea solution (0.15–0.25 M) is placed on the tongue [14, 15]. However, intake studies reveal that newborns consume similar amounts of 0.18–0.48 M urea in water or in a weak sucrose solution compared to the diluent alone [24, 25]. Differential consumption of bitter urea solutions does not occur until infants are approximately 2 weeks of age [26] and is evidenced throughout childhood by a general avoidance of bitter-tasting foods. Together, the orofacial and consumption studies suggest that intake regulation of bitter solutions may mature postnatally.

Recent research in adults and children has focused on understanding the role genes play in individual differences in sensitivity to bitter tastes. Of the 25 human bitter taste receptor genes currently identified, *TAS2R38* is the most commonly studied (for a review see [27]). Polymorphisms in the genes that encode this receptor determine much of the variation in taste sensitivity for a class of bitter-tasting chemicals that includes synthetic thiourea compounds (e.g., propylthiouracil [PROP]) and natural plant toxins (e.g., goitrin) found in cruciferous vegetables such as broccoli [28]. Due in part to polymorphisms on the *TAS2R38* gene, some individuals have a high sensitivity threshold for this class of bitter tastes, while others have lower thresholds and as a result are more sensitive to the bitterness in cruciferous vegetables [29]. In addition to these individual differences, psychophysical studies have shown that PROP sensitivity appears to decrease with age. Children heterozygous for a *TAS2R38* variant perceived lower concentrations of this bitter chemical than did heterozygous adolescents, who in turn detected lower concentrations than heterozygous adults [30, 31]. Such sensitivity to this class of bitter tastes may contribute to reduced acceptance of cruciferous vegetables during childhood.

Preference for sweet tastes is thought to have evolved to attract us to energy-producing sugars that are important for growth and development

Evolution, Today's Obesogenic Environment, and Sensory Learning: A Bitter-Sweet Story

How do we explain children's biological predispositions to prefer sweet-tasting and dislike bitter-tasting foods, even though they lead to maladaptive outcomes that threaten health? Looking back in our evolutionary history reveals that human's current taste perceptions and preferences have been largely shaped by the ecological niches of our evolutionary ancestors. In order to adapt to specific environments that contain some types of food but not others, our sense of taste has changed and, by extension, so has our genome. Early hominoids used their sense of taste to identify nutritious food items among an expansive dietary repertoire. Preference for sweet tastes is thought to have evolved to attract us to energy-producing sugars that are important for growth and development.

However, eating can be dangerous – many risks are associated with making poor food selections, including the potentially lethal ingestion of harmful parasites, bacteria, and chemicals. As a result, rejection of bitter likely evolved to prevent ingestion of potentially dangerous substances, such as poisons, many of which we perceive as bitter. Although these biological predispositions were at one time adaptive, helping us select nutrients and avoid toxins, today preferences for sugary foods and avoidance of bitter vegetables do not provide an adaptive advantage in environments with easy access to a variety of palatable, energy-dense foods and safe fruits and vegetables.

Over the past century, significant changes in our food environment have occurred, including an increase in the number of fast food restaurants and availability of low-cost, energy-dense food options. These changes have been fueled by marketing strategies that target children's inborn preferences for sweet taste [32]. Children can increase their preference for a food product after only a single exposure to a commercial, and this is strengthened with repeated exposures. In turn, these preferences affect their product purchase requests, which ultimately influence their parents' purchasing decisions [33].

The marketing influence on children's food preferences is of particular concern for a number of reasons. First, as discussed above, we do not need to encourage consumption of unhealthful foods, given that children are already predisposed to preferentially consume them. Not only are children attracted to the sweet taste of sugar in these foods, but the presence of sugar can also effectively suppress or mask the bitterness [34, 35] that is inherent in some foods and beverages (e.g., caffeinated energy drinks) that children would otherwise avoid.

Second, through familiarization with sweetened versions of foods and beverages that are not inherently sweet-tasting, such as yogurt, milk, or cereal, children develop an expectation that foods should taste sweet [36]. As a result of the intrinsic plasticity of the taste system, prefer-

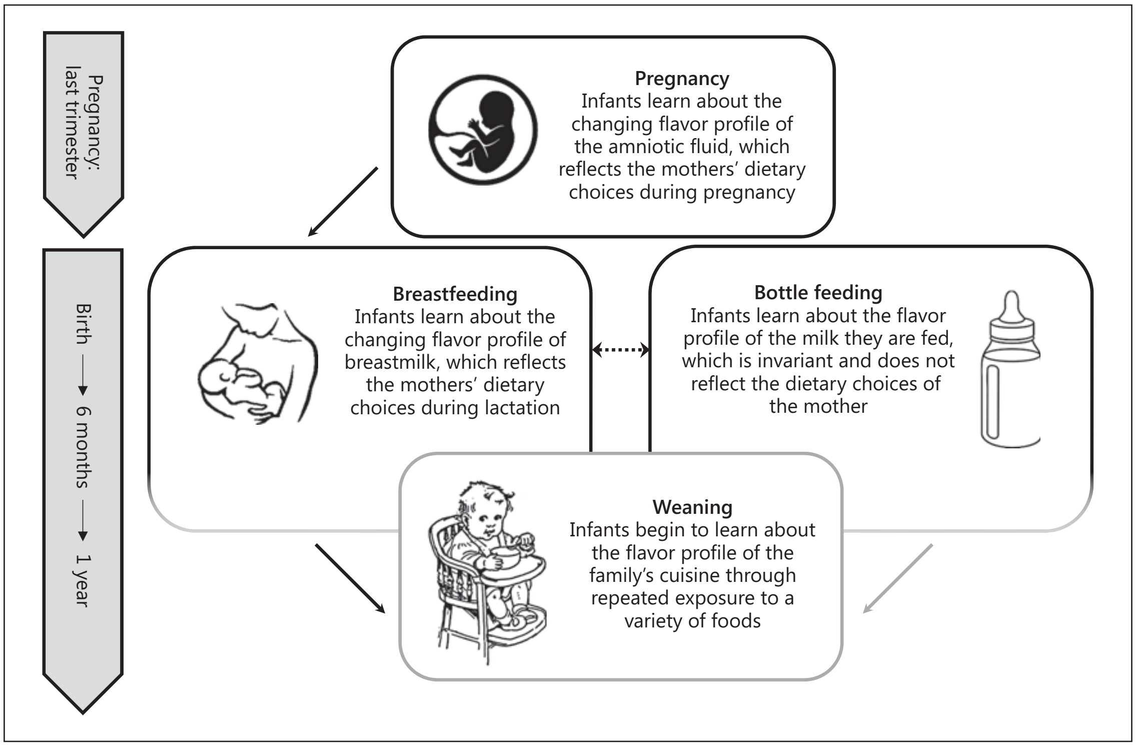

Fig. 2. Flavor experiences during pre- and postnatal development. Common flavors are initially experienced during the fetal period in utero, during postnatal feeding, and during weaning. After birth, the American Academy of Pediatrics recommends feeding only breast milk for the first 6 months of life, followed by a combination of solid foods and breast milk until the infant is at least 1 year old. This gradual transition to a diet consisting primarily of solid foods is represented by the gradated borders in the figure. Breastmilk serves to bridge the flavor experiences during the fetal period to those at weaning (represented by solid black arrows). Many mothers choose to feed their infants formula exclusively, or to feed a combination of breastmilk and formula (as represented by the dotted double arrow). In contrast to the varied sensory experiences of breastmilk, the flavor of formula is monotone and lacks the volatiles of the foods of the mother's diet. These experiences nevertheless affect infants' acceptance of similar flavors at weaning (as represented by the solid grey arrow).

ences for sweeter-tasting foods and beverages are readily acquired through early exposure to sweet taste. For example, longitudinal studies have shown that newborn infants who were regularly fed sugar water preferred significantly higher concentrations of sucrose solutions 2 years later compared to those who had no such experience [37]. Although correlational, these studies suggest that early dietary exposure to sweet foods is associated with later enhanced acceptance of sweet tastes. However, the opposite is also true: just as children's preferences for sweet-tasting foods can be strengthened, preferences for healthful foods can increase as a result of early exposure to the flavors of these foods.

Accumulating evidence suggests that, starting before birth and continuing throughout development, repeated and varied opportunities to learn about the flavors of healthful foods increase later acceptance and consumption of these foods [38]. During fetal development, the intrauterine environment is rich in odor volatiles (i.e., flavors) that change as a function of the mothers' diet. As discussed above, it is likely that the fetus is sensitive to and learning about this ever-changing flavor profile; by the last trimester the taste and olfactory receptors are functional, and the fetus is actively swallowing between 500 and 1,000 mL of amniotic fluid each day [39]. After birth, infants are exposed to a diet that is typically solely milk-based, consisting of breast milk, artificial milk (formula), or both. While the flavor of breast milk, like amniotic fluid, reflects the mother's diet, the invariant flavor profile of formula does not (Fig. 2).

Amniotic Fluid and Breast Milk

A wide variety of flavors ingested by the mother are transmitted to amniotic fluid during pregnancy and to breast milk during lactation, including garlic [40], vanilla [41], anise [42], and carrot [43]. This ongoing exposure to the flavors within amniotic fluid and breast milk biases the infant's flavor preferences for these foods. In one study, mothers consumed carrot juice either for 3 consecutive weeks during the last trimester of pregnancy, or during lactation, while those in a control group drank water during pregnancy and lactation and avoided carrots [43]. Infants exposed to the target flavor, either prenatally or postnatally, preferred carrot-flavored relative to plain cereal, whereas the control group showed no such preference. Further work in non-human animals has replicated these effects and has additionally shown that dogs exposed to aniseed throughout the perinatal period (i.e., pre- *and* postnatal exposure) displayed greater flavor preferences for aniseed at weaning than those exposed to aniseed either pre- *or* postnatally [44].

These results support the contention that the continuity of flavor experiences provided by breastfeeding helps with the transition to solid foods at weaning. This is further supported by findings that breastfed infants are more accepting of fruit than are formula-fed infants, but only if their mothers regularly ate this food during lactation [45]. Breastfed children may also be more willing to accept novel foods [46] and less picky as they grow older [47, 48], especially if their mothers eat a varied diet, which provides a more varied flavor profile in breast milk.

Formula

Infants who are exclusively formula-fed often receive just one type of formula, which limits their exposure to varied flavor experiences [49]. Despite the lack of flavor variety, different types and brands of formulas vary in their characteristic flavor profile, due to differences in their composition and processing [50]. For example, cow-milk-based formulas (CMFs) are described as having low levels of sweetness, with sour and cereal-like characteristics, whereas soy-protein-based formulas have sweet, sour, and bitter tastes. Extensively hydrolyzed protein formulas (ePHFs), the feeding regimen of choice for formula-fed infants who cannot tolerate intact proteins, have high levels of free amino acids, because its proteins are broken down by enzymes. These free amino acids impart a savory, bitter, and sour taste profile, as well as unpleasant odor volatiles (e.g., sulfur volatiles that are found in cruciferous vegetables, such as broccoli [51, 52]). Yet, infants fed ePHF early in life readily learn to accept its "off" flavors [53].

By taking advantage of the inherent differences in the flavor profiles among these formulas, researchers have shown that infants develop flavor preferences that reflect the type of formula they are fed. Compared to infants fed CMF, those fed ePHF ate more savory-, sour-, and bitter-tasting infant cereals at a faster rate and showed fewer facial expressions of distaste during feeding [54]. Moreover, ePHF-fed as well as breastfed infants were more likely to display positive facial reactions to savory-tasting cereal, perhaps because breast milk [55] and ePHF [56] are both high in the savory amino acid glutamate. Other research has shown that the length of time infants are fed ePHF influences their responses to savory food; those fed ePHF for at least 3 months showed greater acceptance of a savory broth relative to a plain broth [57]. Evidence shows that these early preferences can be long-lasting. Several years after the last formula exposure, children fed ePHF during infancy were more likely to prefer a sour-tasting apple juice than were children fed CMF [58]. They were also more likely to preferentially consume broccoli, which has flavor notes similar to ePHF [58]. In combination, these studies reveal that the tastes to which infants are exposed during formula feedings affect their acceptance of foods at weaning. However, if these flavors are not part of the family's diet, infants may not reap the benefits of this early sensory learning. Rather, preferences for the foods that the family eats will be acquired at weaning through repeated exposure.

Children require 8–10 exposures to the taste of a food in order to increase acceptance of it

Complementary Feeding: Increasing Preferences for Fruit and Vegetables

At weaning, children transition from a milk-based to a mixed diet that consists of breast milk or formula and a variety of complementary foods. With the milk-based diet, infants learn to prefer foods through repeated exposure (with formula) or through exposure to a variety of flavors (with breast milk). The same is true for children at weaning: converging evidence from several experimental studies indicates that children require 8–10 exposures to the taste of a food in order to increase acceptance of it. It is important to note, however, that increased *intake* does not always coincide with increased *liking* [45]. Even when infants begin to consume more of a food after repeated exposure, they may continue to display negative facial responses (such as squinting) while eating it. Because these

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negative orofacial responses persist after increased acceptance, parents are less likely to offer the food again [59]. To produce shifts in liking that mirror the changes in intake, exposure needs to continue beyond acceptance until liking occurs (i.e., when the infant begins to show fewer facial expressions of distaste) [45, 60].

Relative to merely repeating exposure to the same food, exposing infants to a variety of flavors has the added advantage of promoting infants' willingness to consume novel foods. As shown in Figure 3, 8 days of exposure to a variety of vegetables increases acceptance of a novel-tasting vegetable [61, 62] but not of a novel fruit [61]. Similarly, 8 days of exposure to a variety of fruits increases acceptance of a novel fruit but not of a novel green vegetable [61]. It appears that the variety of foods presented must share some flavor characteristics of the novel food in order to increase its acceptance. More recent research has shown that exposure to flavor variety continues to be effective in increasing acceptance of fruit between 4 and 8 years of age [63]. However, this study did not find a similar increase in children's preferences for vegetables, which suggests that shifting older children's preference for vegetables may require other strategies such as associative conditioning [64].

It appears that additional factors may moderate the ease with which infants acquire flavor preferences for healthful foods, such as personal characteristics of the child. For example, children who were high in approach temperament were less likely to express facial expressions of distaste (i.e., gape) and consumed more of a bitter green vegetable [65]. Infants with approach temperaments may be more likely to try a greater variety of fruits and vegetables before the onset of neophobia at around 2 years of age. As discussed above, we are also gaining a better understanding of the molecular mechanisms underlying individual differences in taste sensitivity. For example, because of genotype differences, some individuals are more sensitive to the bitter taste of some vegetables and as a result may be likely to eat these foods (e.g., [29, 66]). Yet another factor shown to be important is the parents' feeding style. Osborne and Forestell [63] found that when children were exposed to a variety of fruits and vegetables, they were less likely to develop a preference for a novel fruit when their mothers reported pressuring them to eat. Thus, it appears that early and repeated sensory experiences, child temperament, taste receptor genotype, as well as the quality of mother-child interactions during feeding are just a few of the factors that interact to determine food preferences during childhood.

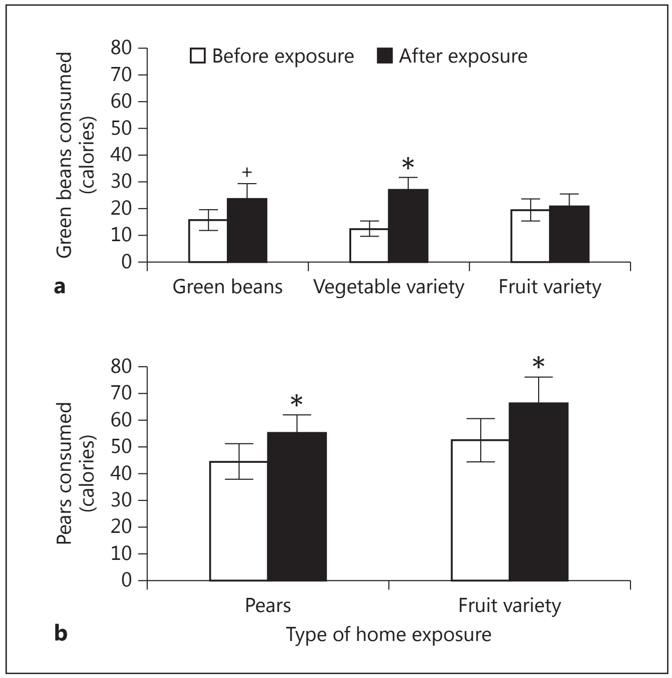

Fig. 3. Infants' intake of green beans (**a**) and pears (**b**) before (white bars) and after (black bars) an 8-day home exposure period in which they were fed green beans, a variety of orange and green vegetables, a variety of fruit, or pears. Infants increased their intake of green beans if they were fed green beans or a variety of vegetables, but not fruit, at home. They also increased their intake of pears if they had been fed pears or a variety of fruit at home. This suggests that, for flavor variety to increase consumption of a novel vegetable, there must be some overlap between the flavor profiles of the variety of foods fed and the novel food [61]. * Significant difference at $p < 0.05$. + Significant difference at $p < 0.08$.

Final Remarks

While no single factor is responsible for the dramatic increases in overweight and obesity in the US over the past century, it is generally accepted that the consumption of sugar-sweetened products, especially beverages, is causally linked to increases in risk of chronic diseases, including type 2 diabetes, cardiovascular disease, hypertension, and stroke [67]. This is concerning because children are born with biological predispositions to preferentially consume sweet-tasting foods and beverages instead of other more healthful foods, such as green vegetables.

Whether this early proclivity for sweet tastes leads to later unhealthy dietary habits depends in part on the child's early sensory experiences. Health care providers should encourage pregnant and nursing women to consume healthful diets with a variety of flavors. Infants who are formula-fed should be exposed to a variety of flavors, particularly those associated with fruits and vegetables, while the mother is pregnant and again at weaning. Although we cannot completely change children's innate liking of sweets and disliking of bitterness, we have learned that early sensory experiences, which begin with the flavors of foods the mother eats during pregnancy and lactation, can shape and modify early flavor and food preferences, thereby increasing infants' acceptance of the foods available in their environment. Thus, a mother's healthy diet increases the likelihood that her child will prefer these same healthy foods. Repeated exposure to healthy foods at weaning will maintain and expand these preferences. Infants' healthy dietary repertoire will continue to grow if they are exposed to a variety of healthy foods at weaning and throughout childhood.

To be sure, whether children have the opportunity to learn about healthful flavors early in life depends on many factors. A family's decisions about food purchases and consumption are influenced by a range of socioenvironmental factors, such as culture, financial status, and education (e.g., [68]). An appreciation and a greater understanding of the complexity underlying food choices in families and how these affect the development of children's food preferences will aid in the development of evidence-based strategies and programs to facilitate children's early acceptance of fruit and vegetables.

Disclosure Statement

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